

Self-organized patterns of coexistence out of a predator-prey cellular automaton

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Abstract

We present a stochastic approach to modeling the dynamics of coexistence of prey and predator populations. It is assumed that the space of coexistence is explicitly subdivided in a grid of cells. Each cell can be occupied by only one individual of each species or can be empty. The system evolves in time according to a probabilistic cellular automaton composed by a set of local rules which describe interactions between species individuals and mimic the process of birth, death and predation. By performing computational simulations, we found that, depending on the values of the parameters of the model, the following states can be reached: a prey absorbing state and active states of two types. In one of them both species coexist in a stationary regime with population densities constant in time. The other kind of active state is characterized by local coupled time oscillations of prey and predator populations. We focus on the self-organized structures arising from spatio-temporal dynamics of the coexistence. We identify distinct spatial patterns of prey and predators and verify that they are intimately connected to the time coexistence behavior of the species. The occurrence of a prey percolating cluster on the spatial patterns of the active states is also examined.

Key words: Cellular automata; Lotka-Volterra; Spatial models; Stochastic models; Predator-prey; Coexistence; Spatio-temporal patterns; Self-organization

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1 Introduction

The most renowned and perhaps the simplest model which displays self-sustained coupled time oscillations in a predator-prey system is the Lotka-Volterra model (Lotka, 1920; Volterra, 1931). In this model individuals of each species are dispersed over an assumed homogeneous space and their spatial positions are not taken into account. It is implicitly considered that any individual can interact with any other with equal intensity and the time evolution of the species populations is given by a set of two ordinary differential equations (Lotka, 1920; Volterra, 1931). These equations may be viewed as mean-field type equations, which do not take into account any spatial correlation between individuals of each species.

If the descriptive level is one where space structure is not relevant then a predator-prey model constructed on the basis of a mean-field approach, such as the Lotka-Volterra equations, can give important qualitative information. It is possible yet to consider more complex prey-predator interactions in the Lotka-Volterra model (Hastings, 1997) or more sophisticated mean-field models (Satulovsky and Tomé, 1994; Satulovsky and Tomé, 1997; Durrett and Levin, 2000; Ovaskainen et al., 2002; Aguiar et al., 2003), which provide the stable coexistence of species and/or stable population cycles. These improvements are qualitatively relevant, since in the original Lotka-Volterra model, the cycles are not stable under small changes of the initial condition, which is not biologically realistic (Hastings, 1997).

However, under certain ecological situations, it is necessary to describe population dynamics by using models which do take into account the spatial localization and discreteness of individuals of each species. In fact, some experimental studies on predation, as the one performed by Huffaker (1958), show that an inhomogeneous space is crucial for the maintenance of self-sustained time oscillations in a prey-predator system. Therefore, to describe the oscillations and species coexistence, it might be important to consider a theoretical approach that goes beyond the mean-field type equations and is able to incorporate the spatial structure of a system. The rôle of space has actually been recognized in several approaches for the description of different population biology problems (Levin, 1974; Tainaka, 1988; Caswell and Etter, 1993; Durrett and Levin, 1994; Satulovsky and Tomé 1994; Hastings, 1997; Hanski and Gilpin, 1997; Tilman and Kareiva, 1997; Provata et al., 1999; Liu et al., 2000; Antal and Droz, 2001; King and Hastings, 2003; Aguiar et al., 2003; Carvalho and Tomé, 2004; Szabó and Sznaider, 2004; Stauffer et al., 2005; Nakagiri et al., 2005).

As summarized by Durrett and Levin (1994) there are basically four theoretical approaches on population biology which give descriptions at different levels.

Among them we single out the modeling by means of an interacting particle system (Liggett, 1985; Durrett, 1988; Marro and Dickman, 1999) also known as a stochastic lattice model (Tainaka, 1988; Satulovsky and Tomé, 1994; Marro and Dickman, 1999; Antal and Droz, 2001; Tomé and de Oliveira, 2001) in the context of nonequilibrium statistical mechanics. The main characteristic of this approach is that it is based on spatial-structured models with continuous time Markovian dynamics where individuals are discrete and localized.

In the present work we are concerned with the modeling of a predator-prey system by means of a probabilistic cellular automaton where the individuals are discrete, localized on the sites (or cells) of a lattice (or grid) and interact only with their neighbors (local interactions). The system evolves in time according to a discrete time stochastic Markovian synchronous dynamics (Caswell and Etter, 1993; Tomé, 1994; Tomé and Drugowich de Felício, 1996). In this approach the time is considered discrete and the update is synchronous while maintaining the other features of the description via an interacting particle system. The local rules of the automaton mimic the process of predation, birth and death of individuals of the two species and are inspired by the rules of the contact process (Liggett, 1985; Durrett, 1988; Marro and Dickman, 1999; Tomé and de Oliveira, 2001).

In the following sections we present the model, explain the computational simulation procedure, show the results, and discuss the properties of the active states. Our attention is concentrated on the study of the spatio-temporal dynamics of coexistence of species. We verify that a given spatial distribution of prey and predators is intimately connected to the time coexistence behavior of the species, which may be oscillatory in time (in finite systems) or not.

2 Model

2.1 Probabilistic cellular automata

Our approach in the modeling of a predator-prey system by a probabilistic cellular automaton are based on the following assumptions. First, we consider that the space where the species interact and survive is represented by a regular square lattice with N sites. Each one of the sites can be in one of three states: empty (no individual species present), occupied by at most one individual of the prey species or occupied by at most one individual of the predator species. These states will be represented by a random variable η_i , associated to site i , which takes three values 0, 1 or 2, according whether the site i is empty, occupied by one prey individual or occupied by one predator individual.

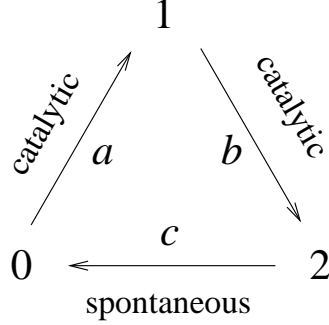


Fig. 1. A scheme of the allowed transitions between distinct states showing the type of process and respective probabilities. The numbers 0, 1, and 2 represent an empty site, a site occupied by a prey individual and a site occupied by a predator individual, respectively.

Each site can assume one state at each time step and the transitions between the possible states, which occur in successive instants of time, obey stochastic local rules that define the prey-predator interaction in a local level. We assume that the transitions from one state to another distinct state must obey the clockwise cyclic ordering shown in Figure 1. The counterclockwise cyclic ordering is forbidden. This assumption implies that the model is microscopically irreversible or that it lacks detailed balance (van Kampen, 1981; Tomé and de Oliveira, 2001). Prey can proliferate just on empty sites; prey give place to predator in the predation process, where it is implicit that a predator reproduces and the prey dies; and a predator can die leaving an empty site. The empty sites can be seen as the resource of food for prey surveillance and proliferation. The process of death of predator complete this cycle reintegrating these resources to the system. Two of the transition rules are catalytic: the birth of prey in a empty site is conditioned to the existence of prey in its neighborhood on the lattice; and the birth of predator in a site occupied by prey is conditioned to the existence of predators in its neighborhood. The process of death of predator is spontaneous, that is, it occurs independently of the states of the neighbors. The conditions for the survival of the species are the same in any region of the space implying that the rules are the same for any site of the lattice. The three processes, the birth of prey, birth of predator and death of predator, comprehend, at a microscopic level, the same reactions involved in the Lotka-Volterra model and are associated to the parameters a , b , and c , respectively.

Let us denote by $P_\ell(\eta)$, the probability of state $\eta = (\eta_1, \eta_2, \dots, \eta_N)$ of the system, at time ℓ . As we will consider a Markovian discrete time and discrete space process the evolution equation for the probability is

$$P_{\ell+1}(\eta) = \sum_{\eta'} T(\eta|\eta') P_\ell(\eta'), \quad (1)$$

where the sum is over all possible states of the system, and $T(\eta|\eta')$ is the conditional transition probability from a state η' to state η , given that at the previous time step the system was in state η' . Since we would like to model the system using a cellular automaton, the update of the sites is synchronous. The global transition probability $T(\eta|\eta')$ is written as the product of the transitions probabilities for each site

$$T(\eta|\eta') = \prod_{i=1}^N w_i(\eta_i|\eta'), \quad (2)$$

where we have denoted by $w_i(\eta_i|\eta')$ the probability that site i assumes the state η_i given that the system is in state η' at the previous time. We observe that $T(\eta|\eta')$ can be written as a product because the state assumed by each site in a given time step ℓ is independent of the states assumed by the other sites. We also remark that from the property that the distribution probability is normalized, the following properties must be held

$$w_i(\eta_i|\eta') \geq 0 \quad \text{and} \quad \sum_{\eta_i} w_i(\eta_i|\eta') = 1. \quad (3)$$

A probabilistic cellular automaton is then defined by just giving the set of transition probabilities, or local rules, $w_i(\eta_i|\eta')$.

2.2 Predator-prey probabilistic cellular automaton

Here we describe the probabilistic cellular automaton for the predator-prey system. Some aspects of this automaton has been considered in a preliminary study by Carvalho and Tomé (2004). A site i of a regular square lattice is updated at each time step by considering its interaction with its neighborhood defined as the four nearest neighbor sites at north, east, west and south. The lattice is synchronously updated and each site in the lattice changes its state according to the set of transition probabilities, or local rules, $w_i(\eta'_i|\eta)$ defined as follows.

Birth of prey. If a site i is empty, $\eta_i = 0$, then it can be occupied by a prey individual if there are individuals of the same species in its neighborhood. The probability of the transition $0 \rightarrow 1$ is equal to $(a/4)$ times the number $N_{1,i}$ of prey individuals present in the four sites of the neighborhood. No birth occurs in the absence of prey, which means that this is a catalytic process.

Predation and birth of predator. The predation occurs when a given site i is occupied by prey, $\eta_i = 1$, and there are predators in its neighborhood. At the same time a predator is born at site i . The probability of the transition

$1 \rightarrow 2$ is equal to $(b/4)$ times the number $N_{2,i}$ of predator individuals in the four sites of the neighborhood. No death of prey and simultaneous birth of predator occur in the absence of predators, which means that this is also a catalytic process.

Death of predator. The death of predator occurs spontaneously, that is, it does not depend on the state of the neighboring sites. In this process a site i which is occupied by a predator, $\eta_i = 2$, is evacuated with probability c , that is, the probability of the transition $2 \rightarrow 0$ is equal to c .

Formally we may write the transition probabilities corresponding to a generic site i as follows

$$w_i(1|\eta) = \frac{a}{4}N_{1,i} \frac{(\eta_i - 1)(\eta_i - 2)}{2} + (1 - \frac{b}{4}N_{2,i}) [\eta_i(2 - \eta_i)], \quad (4)$$

$$w_i(2|\eta) = \frac{b}{4}N_{2,i} [\eta_i(2 - \eta_i)] + (1 - c) \frac{\eta_i(\eta_i - 1)}{2}, \quad (5)$$

and

$$w_i(0|\eta) = c \frac{\eta_i(\eta_i - 1)}{2} + (1 - \frac{a}{4}N_{1,i}) \frac{(\eta_i - 1)(\eta_i - 2)}{2}. \quad (6)$$

They are better viewed in the following matrix

$$\begin{pmatrix} 1 - aN_{1,i}/4 & 0 & c \\ aN_{1,i}/4 & 1 - bN_{2,i}/4 & 0 \\ 0 & bN_{2,i}/4 & 1 - c \end{pmatrix} \quad (7)$$

where each entry of the matrix represents the transition probability from the state defined by the column index (0, 1, or 2) to the state defined by the row index (0, 1, or 2).

These local rules represent the interactions of a system of particles on a lattice. They have some similarities with the local rules of the contact process (Liggett, 1985; Durrett, 1988; Marro and Dickman, 1999; Tomé and de Oliveira, 2001), although here we have a three state discrete time Markovian process whereas the contact process is a two state Markovian continuous time process. The dynamics defined by the above rules leads to active states in which prey and predator coexist and to absorbing states in which the system become trapped.

Empty absorbing state. If a state devoid of prey is reached, there will be no birth of predator and, since the death of predators is spontaneous, a state devoid of individuals of any species will be attained. The system is then trapped

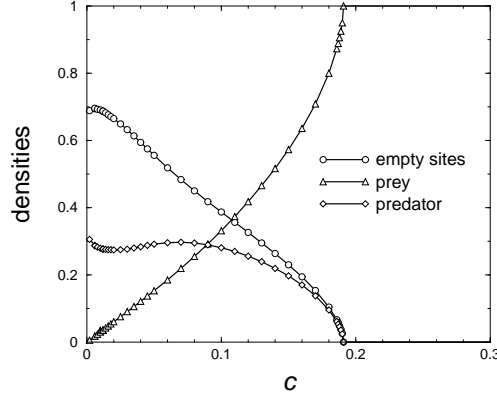


Fig. 2. Densities of prey, predator and empty sites versus c for $p = 0$.

in this empty state where both species have been extinct. This state, however, does not occur due to the abundant population of prey.

Prey absorbing state. If a state devoid of predator is reached and prey have not been extinct then, prey will reproduce until they will cover the entire lattice. The system is then trapped in this prey absorbing state.

The presence of the absorbing states implies the lack of detailed balance which means that the model is intrinsically irreversible (van Kampen, 1981; Marro and Dickman, 1999; Tomé and de Oliveira, 2001).

3 Simulation of the cellular automaton

3.1 Active states

In order to analyze the behavior of the predator-prey system modeled by the cellular automaton we perform numerical simulations. We consider a square lattice of $N = L^2$ sites and use periodic boundary conditions, that is, opposite edges of the lattice are connected forming a torus. The initial configuration is randomly generated by placing prey with probability $1/3$, predators with probability $1/3$ and leaving the sites empty with probability $1/3$. Each site is updated, synchronously and independently, according to the rules (4), (5) and (6). Most of our results were obtained for lattice sizes with $N = 160 \times 160$ sites.

Each update of the lattice corresponds to one time step. The first steps in the simulation are discarded, since they correspond to the transient regime where microscopic configurations are not yet being generated according to the appropriate probabilities specified by the given set of parameters a , b and c .

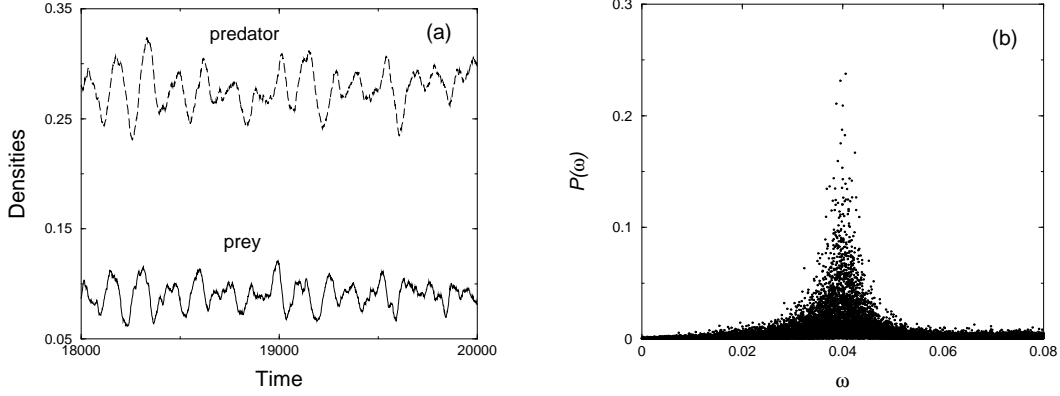


Fig. 3. (a) Densities of prey and predator as a function of time for $p = 0$ and $c = 0.03$ (oscillating state). (b) Corresponding power spectrum for the density of prey as a function of the frequency ω . Results obtained for a lattice of size 160×160 .

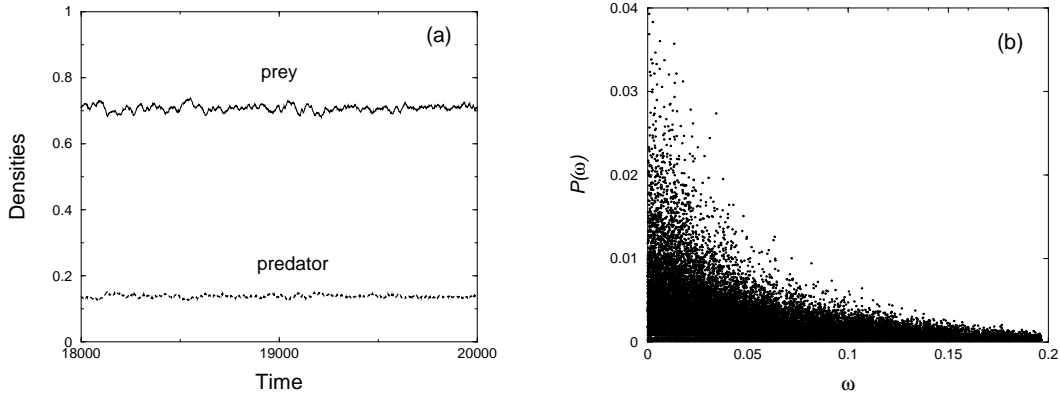


Fig. 4. (a) Densities of prey and predator as a function of time for $p = 0$ and $c = 0.17$ (nonoscillating state). (b) Corresponding power spectrum for the density of prey as a function of the frequency ω . Results obtained for a lattice of size 160×160 .

The density of prey ρ_1 , the density of predator ρ_2 and the density of empty sites $\rho_0 = 1 - \rho_1 - \rho_2$ are computed for each time step.

We restrict ourselves to the values of a , b and c such that $a + b + c = 1$. This allows us to introduce the following parametrization

$$a = (1 - c)/2 - p \quad \text{and} \quad b = (1 - c)/2 + p, \quad (8)$$

with $-1/2 \leq p \leq 1/2$. The parameter c , the death of predators, is restricted to $0 \leq c \leq 1 - 2|p|$.

Fixing the value of p we have found that the system evolves in time and eventually reaches either an absorbing prey state or an active state. An absorbing prey state, which is characterized by $\rho_1 = 1, \rho_2 = \rho_0 = 0$, occurs for high values of c . As c is decreased the active state, where $0 < \rho_1 < 1$,

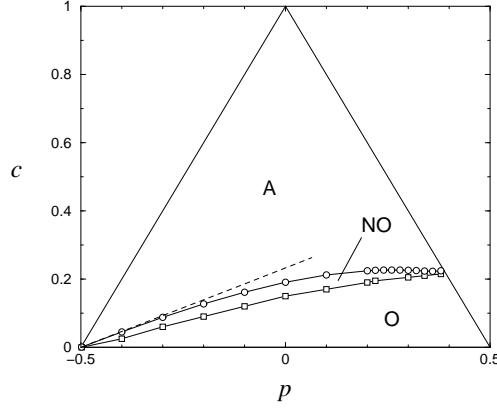


Fig. 5. Space of parameters, or $p - c$ diagram, showing regions corresponding to three states: prey absorbing (A), active nonoscillating (NO) and oscillating (O). The straight dashed line represents the critical transition line of the contact process for the predator-prey system without vacant sites (see text).

$0 < \rho_2 < 1, 0 < \rho_0 < 1$, is reached. The behavior of the densities of prey, predators and empty sites versus c , for $p = 0$, is shown in Figure 2.

Figures 3 and 4 exhibit two possible time evolutions of the densities of prey and predators corresponding to active states. For small values of c the time series for the population densities show an oscillatory behavior, as can be seen in Figure 3. For larger values of c the oscillations disappear and the observed density variation in this time series are just stochastic fluctuations, as shown in Figure 4. Typical power spectra $P(\omega)$ related to the density of prey, for the oscillating and nonoscillating cases, are also shown in Figures 3 and 4, respectively. The power spectra related to the density of predator (not shown) are similar. The presence of a prominent and well defined peak in the power spectrum of Figure 3 at a nonzero frequency characterizes an oscillating behavior. The power spectra for the population densities of predators and prey have a peak at the same frequency implying that the oscillations of the two species are coupled. In contrast, the monotonic decreasing in the power spectrum with frequency characterizes a random fluctuation related to the nonoscillating active state, as shown in Figure 4.

3.2 Space of parameters

The parametrization defined by equation (8), which implies the condition $0 \leq c \leq 1 - 2|p|$, means that the possible values of c and p defining the space of parameters, or the $p - c$ diagram, are restricted to the triangle drawn in Figure 5. Depending on the values of the parameters c and p one of the three possible states, prey absorbing and the two active states, can be reached as shown in Figure 5. This diagram was obtained by numerical simulation with

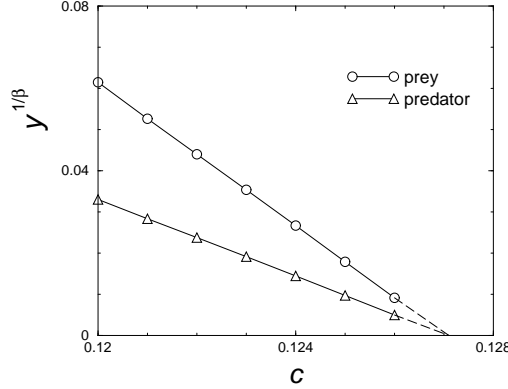


Fig. 6. The quantity $y^{1/\beta}$, where y represents either the predator density ρ_2 or $1 - \rho_1$, where ρ_1 is the prey density, versus c , with $\beta = 0.58$ (Marro and Dickman, 1999). Results correspond to $p = -0.2$.

lattice sizes up to $N = 720 \times 720$ sites. A critical transition line $c_1(p)$ from the prey absorbing state to the active state cross the entire $p - c$ diagram starting from the left corner of the triangle and ending at the opposite side. The active region of the $p - c$ diagram is divided into two regions, the oscillating and nonoscillating, by a line $c_2(p)$ that also starts at the left corner and ends at the opposite side of the triangle.

The presence of a peak at a nonzero frequency in the power spectrum was used to estimate the transition line on the $p - c$ diagram between the regions corresponding to the oscillating active state and the non-oscillating active state. Fixing the value of p and departing from the oscillating region of the diagram we increase the value of c . The transition to the nonoscillating active region occurs at a value c_2 where the peak in the power spectrum disappears. For instance, for $p = 0$, we get $c_2 \approx 0.15$ at which point the prey density assumes the value $\rho_1 \approx 0.58$. It is worth to note that the oscillatory behavior is observed in finite systems what implies that the oscillations occur in a local level (Carvalho and Tomé, 2004).

To analyze the transition between the regions of the diagram corresponding to the active state and the prey absorbing state we have considered large lattice sizes. Also, we have modified the simulation procedure by not allowing the extinction of the species: if the number of prey vanishes then a prey individual is created in an empty site chosen at random; if the number of predators becomes zero then we randomly choose a site occupied by prey and replaces it with a predator. This makeshift was required mainly in the transient regime where greater amplitudes and fluctuations are attained. A spurious entrance in the absorbing state was avoided by the makeshift and the conditions for a stable regime were provided.

We expect that near the transition from the active state to the prey absorbing

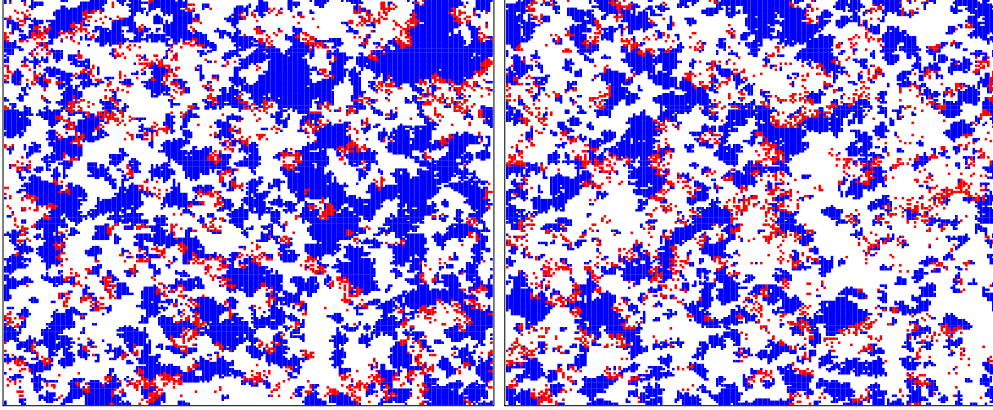


Fig. 7. Snapshots of the lattice for $p = 0.3$ and $c = 0.13$ (inside the oscillating region of the $p - c$ diagram) taken at a maximum of prey (left) and a minimum of prey (right). Results obtained for a lattice of size 160×160 . The blue points represent sites occupied by prey, the red points by predators and the white points are empty sites.

state the densities of predator and prey obey the following asymptotic behavior $\rho_2 \sim (c_1 - c)^\beta$ and $1 - \rho_1 \sim (c_1 - c)^\beta$, respectively, where β is the critical exponent associated with the order parameter (Marro and Dickman, 1999). From Figure 6 we can see that, fixing p , the densities of predators and prey indeed obey these relations. With this assumption we were able to estimate the localization of the critical line $c_1(p)$ from the active state to the absorbing state by fitting a straight line to the data points of $(1 - \rho_1)^{1/\beta}$ and $\rho_2^{1/\beta}$ versus c . It was assumed that the critical exponents associated to the transition from the active state to the absorbing state belong in the direct percolation universality class (Grassberger, 1982), which gives a critical exponent $\beta = 0.58$ in two dimensions (Marro and Dickman, 1999).

3.3 Contact process limit

As the probabilities of death and birth of predators become negligible (c and b small, corresponding to the region around the left corner of the $p - c$ diagram of Figure 5), the dynamics of the model is dominated by the birth of prey. It means that any empty site is quickly converted into a site occupied by prey. Since the spontaneous death of predator create empty sites and these in turn are almost instantaneously occupied by prey, one may say that predators are being spontaneously “converted” into prey. We may thus replace the two reactions $2 \rightarrow 0$ and $0 \rightarrow 1$ by just a spontaneous reaction $2 \rightarrow 1$. The whole process is therefore reduced to a contact process with two states (1 and 2, or predator and prey) with a spontaneous reaction $2 \rightarrow 1$ with probability c and a catalytic reaction $1 \rightarrow 2$ with probability b . Equivalently, the spontaneous process occurs with rate 1 and the catalytic process with creation rate $\lambda = b/c$. For $\lambda < \lambda_c$, where λ_c is the critical creation rate, the stationary state is the

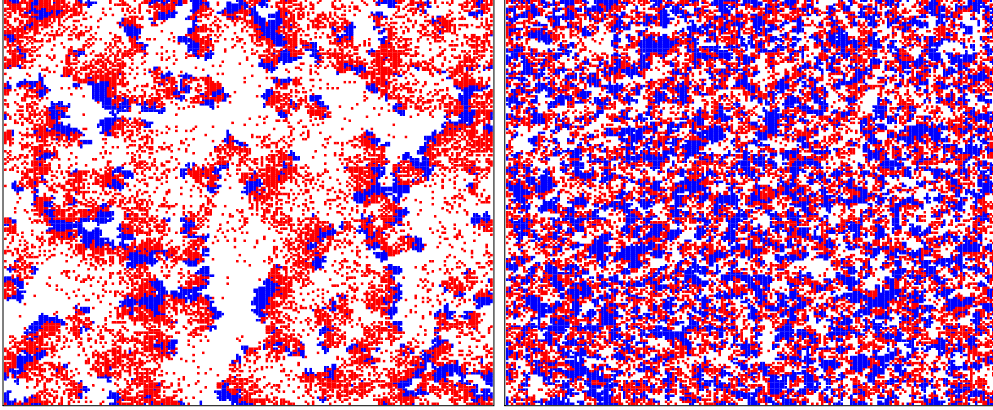


Fig. 8. Snapshots of the lattice (inside the oscillating region of the $p - c$ diagram) for $p = 0$ and $c = 0.03$ (left) and $p = 0$ and $c = 0.10$ (right). Results obtained for a lattice of size 160×160 . The blue points represent sites occupied by prey, the red points by predators and the white points are empty sites.

absorbing state. Then, for $b < \lambda_c c$ the system displays the prey absorbing state. For small values of c the critical line is given by $b = \lambda_c c$ or, equivalently, $c = (p + 0.5)/(\lambda_c + 0.5)$. Our numerical simulations confirm this conjecture if we use the value $\lambda_c = 1.65$ for the contact process in a square lattice (Marro and Dickman, 1999). This result can be seen on the diagram of Figure 5 where we have plotted the line $c = (p + 0.5)/(\lambda_c + 0.5)$. This line is tangent to the critical transition line $c_1(p)$ at the left corner point of the triangle.

4 Spatial patterns and coexistence of species

There are basically three types of spatial pattern formation coupled to the coexistence of species. They are described as follows.

Many cluster landscape oscillations. For $p > 0$ ($a > b$), typical spatial patterns connected to the time oscillations can be seen in Figure 7. We have analyzed the snapshots of the lattice taken at successive instants of time. In this figure, just the snapshots corresponding to the maximum of prey and to the minimum of prey population are shown. It can be observed that they are very similar, and resemble a space covered with patches occupied by the different species. It is noticeable the presence of clusters of prey of different sizes including a very large one, almost percolating the lattice, when the maximum prey population is attained; after this instant of time, the largest clusters begin to breakdown into small clusters or to have their size reduced, giving room to the predators which then attain their maximum population. From this point on the prey population decreases until it attains its minimum value. Large clusters of empty sites occupy the lattice and predators start dying until they reach their minimum population value. After this, prey begin to reproduce until they

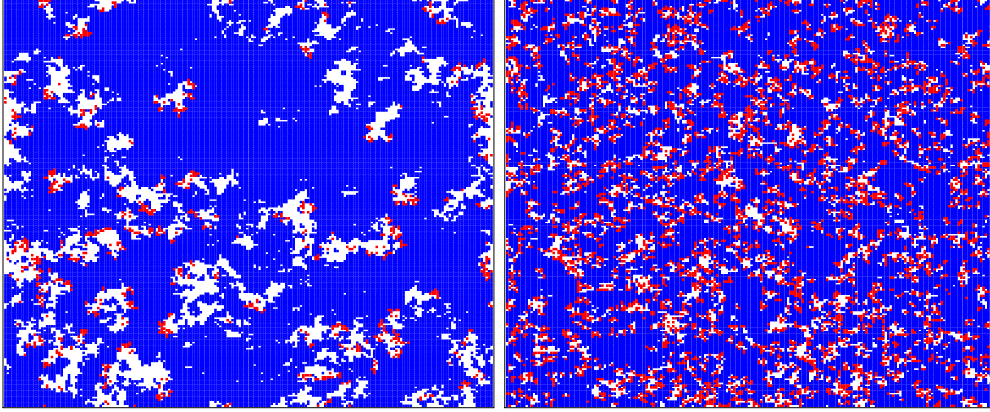


Fig. 9. Snapshots of the lattice for $p = 0.3$ and $c = 0.21$ (left) and $p = 0$ and $c = 0.17$ (right), both inside the nonoscillating region of the $p - c$ diagram. Results obtained for a lattice of size 160×160 . The blue points represent sites occupied by prey, the red points by predators and the white points are empty sites. In both cases the blue points percolate the lattice.

reach a maximum population value closing a cycle of coupled oscillation. We remark that, in each cycle, the maximum of predator follows the maximum of prey.

In the region of the $p - c$ diagram where $p \leq 0$ ($a \geq b$) and for small values of c , the model can exhibit the patterns of coexistence of species shown in Figure 8. For sufficient low values of c the density of predators is appreciable. Predators stay grouped together in small clusters distributed over the entire lattice. The prey reproduce with rate greater than (or equal to) their death rate. Any decrease in prey population by predation is then quickly recovered. As a consequence the amplitudes of oscillations become small, as seen in Figure 3. For a not so small value of c , as that corresponding to the pattern shown in the right panel of Figure 8, the densities of prey and predator still oscillate in time but now the prey population is greater than the predator population.

Prey percolating landscape. For a larger value of c the active nonoscillating region of the $p - c$ diagram is reached. Snapshots of the lattice, showing patterns corresponding to two points in the nonoscillating region of the $p - c$ diagram, are presented in Figure 9. They correspond to the same p values of Figures 7 and 8, but for a greater value of c . In these cases, there are a large cluster of prey that percolates the lattice and small clusters of empty sites and of predators. Let us consider the case $p = 0.3$ and compare the spatial patterns at $c = 0.13$, associated to the active oscillating state (Figure 7), with the pattern at $c = 0.21$, associated to the active nonoscillating state (left panel of Figure 9). We observe one important feature that differentiates the two kind of active states for a fixed value of p .

In one case (active states without oscillations) there is a percolating cluster of prey and in the other (active states with oscillations) spatial patterns do not

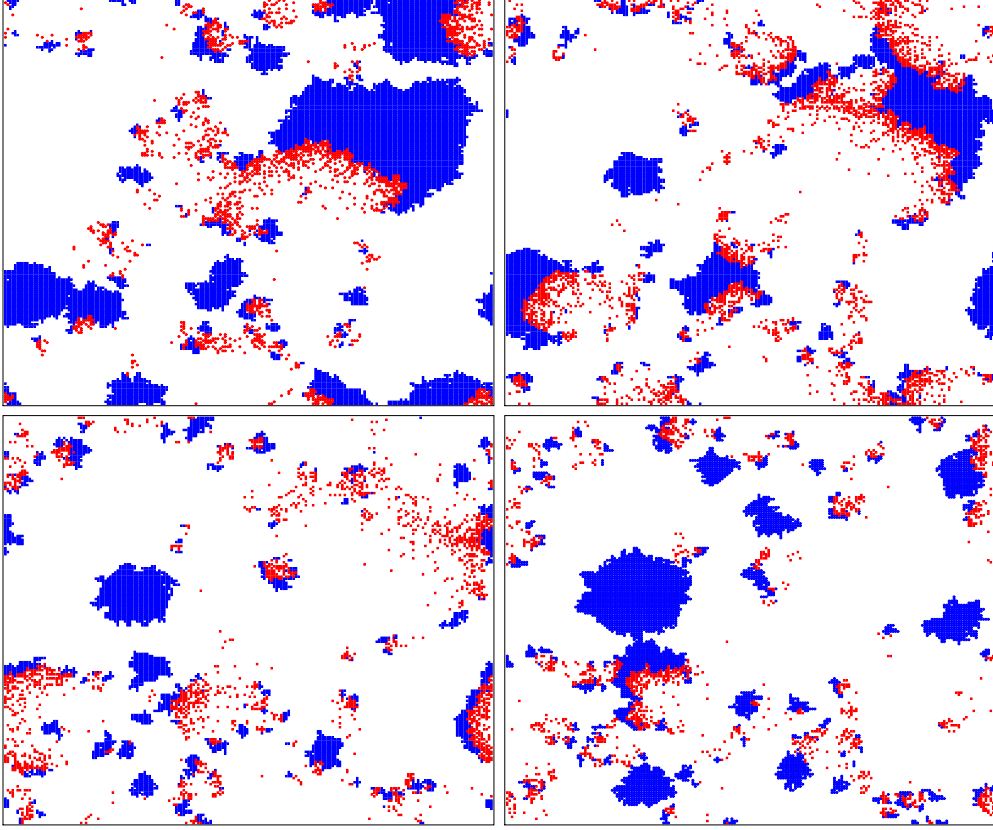


Fig. 10. Snapshots of the lattice for $p = 0.3$ and $c = 0.06$ (inside the oscillating region of the $p - c$ diagram) taken at maximum of prey (top, left), maximum of predators (top, right), minimum of prey (bottom, left), and minimum of predator (bottom, right). Results obtained for a lattice of size 160×160 . The blue points represent sites occupied by prey, the red points by predators and the white points are empty sites.

present a percolating cluster. Similar comparison can be made for $p = 0$ (see right panels of both Figures 8 and 9). Therefore the onset of the nonoscillating active state seems to be associated to the formation of a percolating cluster of prey. Presently, we are analyzing the transition line in the $p - c$ diagram from the active nonoscillating state to the active oscillating state, and its relation with the pattern formation and the percolation theory.

Compact-cluster landscape oscillations. For $p > 0$ ($a < b$) and considering very small values of c , we can observe a special spatial pattern formation connected to the oscillations, as seen in Figure 10. We are considering $p = 0.3$, what implies that the death of prey occurs with probability greater than its reproduction probability. This can lead to a situation where a very small number of prey is present on the lattice (minimum of prey). On the other hand, under this situation, predators can reduce dramatically their reproduction, and even if their probability of death c is small, the predator density can evolve to a very small value (minimum of predators). This fact allows a great increase of the isolated clusters of prey until they become large and compact

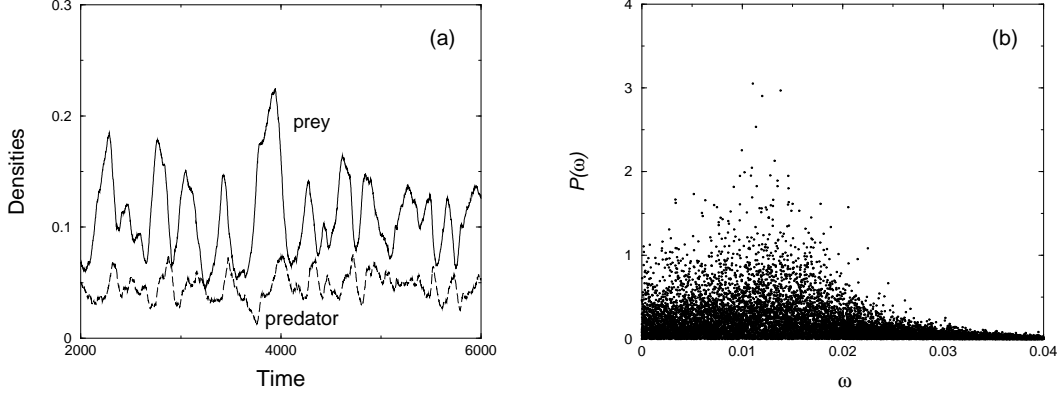


Fig. 11. (a) Densities of prey and predator as a function of time for $p = 0.3$ and $c = 0.06$ (inside the oscillating region of the $p - c$ diagram). (b) Corresponding power spectrum for the density of prey as a function of the frequency ω . Results obtained for a lattice of size 160×160 .

clusters (maximum of prey). These compact clusters keep increasing until they eventually encounter the reminiscent predators or small groups of predators. At this moment the predators eat prey very quickly, reproduce at a high rate, and attain their maximum population. This is an example of the type of a sequence of pattern formation connected to the time oscillations, for set of the parameters, where the predation is highly efficient, the birth prey probability is small and the mean lifetime of predators is high ($c \ll 1$); under these conditions predators are able to practically decimate a large cluster of prey. And then, without food, they start dying, until the situation where small clusters of prey begin to increase and the all succession of above described situations repeat in time with a given characteristic frequency. We observe that a maximum of predator population always follow a maximum of prey population.

The above mechanism leads to most pronounceable amplitudes of oscillations, as can be seen in Figure 11. In this case the period of a cycle is large when compared with the period of a cycle associated to the many cluster landscape oscillations. The large period is the result of a very slow increase in the number of prey ($a \ll b$) which might reach very large values before starting to be decimated by the small number of remaining predator individuals.

All the pattern formation, described above, are self-organized structures (Nicolis and Prigogine, 1977; Haken, 1983; Tomé and de Oliveira, 1989; Hassel et al., 1994) resulting from the spatio-temporal dynamics of the probabilistic cellular automaton. It is important to observe that any macroscopic ordering coming from a microscopic irreversible dynamics is called a self-organized structure. Of course, here, this phenomenon is more evident in the case of the highly inhomogeneous spatial patterns of figure 10, which are coupled to the self-sustained oscillation shown in figure 11.

5 Summary and discussion

We have presented a probabilistic cellular automata with Markovian local rules mimicking the interactions of a predator-prey system. In this description we have considered a regular square lattice where each site can be either occupied by at most one individual of each species or can be empty and the interactions just occur in the neighborhood of a site. Our computational simulations show that the model displays three states, depending on the values of the set of parameters: the absorbing prey state, an active state where both species coexist and their densities are constant in time (nonoscillating active state) and an active state where a self-sustained time oscillation of the prey and predator populations is present.

The time oscillations of prey and predator populations are related to spatial patterns characterized by clusters of prey and predators. In this case, the prey clusters may cover large regions of space but never percolate the lattice. We classified the patterns associated to oscillation in two types. One of them, which was called many cluster landscape, is constituted by a large number of clusters distributed over the entire lattice. The clusters are not compact and may be of a fractal nature. In this case the clusters of prey grow and shrink as the system attains a maximum or a minimum of prey population in a cycle of oscillation. This spatio-temporal behavior is accomplished in a large range of the parameters. The other type of pattern associated to oscillations, which was called compact-cluster landscape oscillations, is characterized by a few number of large compact clusters of prey. In this case, the spatial patterns are very inhomogeneous and they differ among themselves, appreciably, as the maximum and minimum of each species is attained in a cycle. These inhomogeneous patterns occur for small values of the prey birth probability and for very small values of death predator probability (when compared to the predation probability values). Under these conditions predators eat prey so efficiently that they practically decimate all prey clusters becoming then isolated from the few and small reminiscent cluster of prey. Without neighboring prey, they start to die leaving large regions of empty sites; a propitious condition for the growing of the big and compact clusters of prey. Great periods and amplitudes of oscillations are detected. The maximum of predators always follow the abundance of prey in each cycle of oscillations

Our model also predicts a coexistence without oscillations, which was called prey percolation landscape. This regime happens on a small range of the parameters, at values of predator death probability large compared with the ones associated to the oscillating region. In this case the number of prey is large and the spatial pattern is characterized by the presence of a percolating cluster of prey, that is, the prey get together in a extensive and connected region of space.

The results of the predator-prey cellular automaton indicate that the spatio-temporal patterns of coexistence arises from a combination of the Lotka-Volterra basic mechanisms of interaction, the discreteness of individuals and the spatial-structured model. The self-sustained coupled oscillations of prey and predator populations appear, in finite systems, when the death probability of predators is sufficiently small. The coexistence without oscillations appear when this probability is increased. The threshold of the transition between the regime of coexistence of species and the regime where predators have been extincted is enhanced as the predation probability becomes greater than the birth prey probability. For very small values of the predator death probability and high values of the predation probability the spatial patterns associated to oscillations are highly inhomogeneous. The pattern formation, as well as the time oscillations, result from the intrinsic dynamics of the probabilistic cellular automaton. In this sense, they are self-organized structures, that is, the collective interactions of the system of particles in the lattice is able to produces spatio-temporal macroscopic ordering which is self-maintained.

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